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John M. Mandzak
James A. Moore

ABSTRACT. In this paper we present evidence supporting the premise that forest nutrition, nutrient cycling and nutrient management are critical factors for the health of Inland Western forests and for management of the ecosystems. The current state of knowledge suggests that inadequate tree nutrition, particularly potassium shortage, influences tree chemistry such that inadequate plant defensive compounds are produced. Pathogens and insects are unusually successful in attacking such trees. Forest managers have substantial influence on the forest nutritional environment through nearly all types of silvicultural treatments.

INTRODUCTION

In this paper we summarize evidence supporting the premise that nutrition, nutrient cycling and nutrient management are critical factors to consider when assessing Inland Western forest health and ecosystem management.

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The Nature of Inland Western Forests and Current Forest Health Issues

The Inland West is roughly defined for our purposes as an area generally east of the Cascade crest in Washington and Oregon, extending into British Columbia and including the drier portions of the Klamath and Sierra Ranges in Oregon and California east to the Great Plains of the U.S. and Canada. A defining feature of these forests is a midsummer drought period typically most intense in late July through August.

Forest health is currently entwined with the developing concepts of ecosystem management and is thus difficult to separately define. However, there is considerable interest in doing so to determine the future of these forests. In turn, potential future and desired future conditions will shape forest management planning goals. Riitters et al. (1990), stated that no widely accepted definition of forest health exists. Leonard, O'Laughlin, and Marshall presented papers with various definitions and concepts of forest health during a recent symposium on Forest Health in the Inland West (Adams and Morelan 1993). The simplest definition of forest health is the absence of significant diseases and pests or poor tree vigor.

Many authors express a belief that "a crisis in forest health" exists in the Inland West (Leonard 1993; Mutch 1993) and we agree. Several phenomena and symptomatic conditions are listed as proof, such as severe insect outbreaks, extensive root disease and increasing incidence and severity of catastrophic wildfire. Effective fire exclusion in past decades seems to have exacerbated these problems. It is typically pointed out that with the absence of fire, many inland forest types have developed away from open forest conditions previously maintained by frequent natural underburning. The presettlement forests usually were composed primarily of seral species. In contrast, closed canopy, multistoried stands, with a predominance of mid to late successional species are now common. The current stand conditions have a much higher potential for catastrophic stand replacement fires and increased incidence of insects and pathogens resulting in reduced tree vigor and increased mortality rates (Arno 1988; Hungerford et al. 1991).

Inland Western forests exhibited a far different range of conditions in the presettlement period than that observed today. Current forests are more extensive in area and exist on many previously nonforested sites, with more carbon stored as tree biomass (Harvey et al. 1992).

Role of Inorganic Plant Nutrients in Forest and Ecosystem Health

We believe, as do others (Kimmings 1977; Jurgensen et al. 1990), that significant evidence exists to support causality for stress induced by min-

eral nutrient deficiency and consequent implications for Inland Western forest ecosystem health. We agree that carbon and nitrogen are key nutrient elements (Harvey et al. 1994) but we also strongly suggest that other inorganic nutrient elements should be recognized as significant determinants of plant, and therefore forest ecosystem, vigor. We will describe results implicating potassium as an example of a critical "other element." We will also explore how human intervention, by design or not, can affect forest nutrient reserves and consequently inland forest health (Harvey et al. 1989). We presume that the nutritional status of inland forests is outside the historic range of variation since nutrient deficiencies are universal in the region (Mika et al. 1992) and humans have recently excluded fire from forest ecosystems and have often displaced or otherwise removed nutrients during harvesting or silvicultural activities. A more detailed understanding of all the relationships between mineral nutrient status and current forest health status is beyond the scope of this paper and would require more speculation than the authors are comfortable with. We therefore will concentrate on the research needed to improve our basis for understanding these relationships.

OVERVIEW OF NUTRITIONAL PROCESSES

Nutrient Requirements of Plants

An essential inorganic nutrient element for plants is defined as an element required to complete its life cycle. The common list of essential inorganic nutrient elements for green plants includes Carbon(C), Hydrogen(H), Oxygen(O), Nitrogen(N), Phosphorus(P), Potassium(K), Sulfur(S), Calcium(Ca), Magnesium(Mg), Iron(Fe), Manganese(Mn), Molybdenum(Mo), Copper(Cu), Boron(B), Zinc(Zn), Cobalt(Co) and Chlorine(Cl). Other elements such as Sodium (Na), Silicon(Si) or Selenium(Se) have also been demonstrated to be necessary for some plant and animal species.

Concepts of Nutrient Deficiency and Sufficiency

Plants fundamentally are "fixers" of atmospheric carbon. Plants create building block carbon, hydrogen and oxygen molecules and in the process "split" water, releasing oxygen. Forest process models typically use nitrogen reserves in forest ecosystems as a key variable to represent the potential for plant and ecosystem function, vigor and productivity. The relationship or ratio between inorganic nutrient elements such as nitrogen to the quantity of carbon (biomass) that can be fixed (Running and Gower 1991)

is used along with other primary growth factors such as light, oxygen, water, and heat in these process models to predict the ability of a site to fix carbon. In addition to carbon/nitrogen, the relationships between all essential inorganic nutrient elements can be expressed as critical nutrient ratios (Ingestad 1979). Later in this paper we will give examples of the nitrogen/potassium relationships we have been exploring. Since quantities and ratios of 16 or more elements can influence carbon fixation, it is reasonable that inorganic elements can strongly influence plant, and therefore ecosystem, function in a profound manner. Typically though, only a few inorganic nutrient elements limit carbon assimilation and allocation on most individual sites.

Inorganic Plant Nutrients in Inland Forest Ecosystems

The nutrient capital of a forested site is contained in the soil, living and dead plants and animals (Tomlinson and Tomlinson 1990; Buol et al. 1989). The soil forming factors are climate, parent materials, organisms, relief and time, and maybe subsequently indentified human activity. Soils of the Inland West are predominantly young in the time scales of soil formation, primarily because of a relatively recent geologic history of glacial, interglacial, and volcanic activity. Because of the relatively cool and dry climate, mineral weathering and soil development processes occur slowly and the steep terrain limits soil profile development. Current soil properties of the Inland West, including the ability to supply nutrients, are therefore predominantly a function of the accumulated soil organic matter and the relatively unaltered soil parent material reflecting the rock, minerals and geomorphic processes from which the soil profiles were developed. Nitrogen is the only essential inorganic element which is fixed from the atmosphere by plants and microorganisms predominantly on site. Other removals and additions to the nutrient capital occur mostly through precipitation, wind transport, leaching and soil movement.

Brockley et al. (1992), state that "... inadequate nutrition is characteristic of many forests of the Interior Northwest. Nitrogen deficiencies are widespread and serious enough to dominate nutrient management concerns. On many sites, forest management activities and recurring wildfires may exacerbate existing nutritional problems. Because a large proportion of site nutrients may be contained in the forest floor and surface mineral soil, many interior forest soils—those where organic matter is produced, recycled, or replaced very slowly (e.g., dry, cold or fire-damaged sites)—are vulnerable to harvesting or site preparation practices that remove or displace surface organic layers and nutrient rich topsoil (Jurgensen et al. 1990)." Also, the removal of needles and branches in whole-tree harvest-

ing operations will likely have a negative impact on soil nutrients and long-term soil productivity (Kimmins 1977).

Nutritional Implications of Ecosystem Disturbance and Recovery

In the discussion above, location and compartmentalization of inorganic nutrients in the living and dead biomass and soil was described. This is a dynamic process with nutrient transfers occurring in a process termed nutrient cycling (Cole et al. 1967). It is clear that among other effects, nutrient cycling often occurs in ways uncommon in presettlement conditions. These effects can be characterized, at least at this time, as abnormal lack of disturbance. Large volumes of standing live and dead biomass contain much of the inorganic nutrients previously held in the soil, or in the case of nitrogen, there may be higher quantities stored than in conditions receiving regular disturbance (McDonald 1993; Cochran and Hopkins 1991).

Fire—Fire is the primary carbon and inorganic nutrient recycling agent for the majority of forest types in the Inland West (Harvey et al. 1992; Arno 1988). Most nutrient elements are non-volatile; that is, they remain behind in ash (except perhaps in very hot burns of long duration). Nitrogen is volatilized during combustion and is returned to the atmosphere primarily as nitrogen oxides. The greatest risks to nutrient reserves as a consequence of fire are excessive nitrogen volatilization and the potential erosion of nutrient rich ash after very intense fire events.

Windthrow—Windthrow itself does not have a large impact on nutrient reserves since nutrients are returned through decomposition. The danger in the Inland West, though, is that a fire in the resulting downed and heavy fuels can be very intense, leading to excessive soil heating and to the loss of nitrogen and soil organic matter.

Harvesting & Slash Disposal—Effects of harvesting and slash disposal vary widely, depending on site conditions and the specific site treatments. The key point to remember is that nutrients are most concentrated in the fine branches and needles. Bole wood (logs) are relatively low in nutrient content. Whole tree harvesting is a process by which whole trees and attached crowns are transported to landings for processing and disposal. This process can result in significant export of nutrients, which ultimately may need to be replaced by fertilization. Follow-up slash disposal can have a great impact on nutrient capital as well, particularly if very intense slash fires volatilize nitrogen from the slash, duff and upper soil horizons. Dozer and windthrow piling, prior to burning, localizes nutrients, making access to nutrients for the next stand unevenly distributed. Brockley et al. (1992) and Kimmins (1977) provide comprehensive reviews of these topics.

Insects—Insect effects depend on the severity of the infestation and

consequent level of tree mortality. In a mass mortality event, such as by pine bark beetles, effects on nutrient capital can be compared to wind-throw mortality. Defoliation episodes result in accelerated nutrient recycling as nutrient rich foliage is returned to the forest floor as fecal material. Again, no severe loss of nutrient capital may occur, particularly if understory plants and recovering trees quickly reabsorb nutrients.

Root disease—Root disease effects on nutrient capital are relatively undramatic. Mortality occurs at a relatively low rate and is often quite localized such as in *Armillaria* root disease centers.

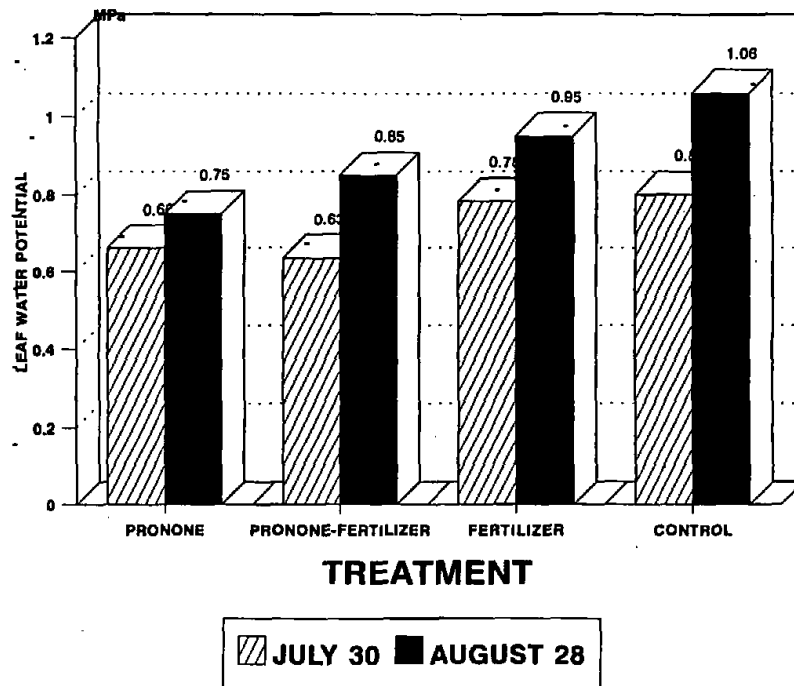
Current Conditions and Studies

Nitrogen concentration in foliage of inland conifers is apparently inadequate for optimum forest growth, based on results in almost all studies completed (Moore et al. 1991; Shafii et al. 1989; Brockley et al. 1992). In addition to the prevailing nitrogen deficiency, potassium (Mika and Moore 1991), sulfur, and micronutrients—particularly boron, iron and magnesium—have also been suggested as deficient on some sites. This list will likely be expanded as investigations continue.

Nutrient and Water Stress Relationships: Insights from Fertilizer and Herbicide Treatments

Soil moisture deficits are clearly another significant limiting factor for growth of inland forests. Data from Montana trials (Mandzak, unpublished), including combinations of herbicide and fertilization treatments, indicate that nutrient status influences water relations and that competition with understory plants affects both water status and foliar nutrient content. Figure 1 shows predawn moisture stress at a typical installation for herbicide removal of competing vegetation (PRONONE), fertilization with a "complete" fertilizer mix, a combined "weed and feed" treatment and no treatment options. Predawn moisture stress in a ponderosa pine (*Pinus ponderosa* Dougl.) stand with a well developed grass and low shrub understory is lowest for the herbicide and greatest for the control treatment, thus indicating substantial interspecies competition for water. It is especially interesting that moisture stress is low after the fertilizer treatment, in spite of substantial increases in conifer foliage and understory biomass. The increased potential for evapotranspiration resulting from the increase in leaf area is presumed to be offset by improvements in plant water control, such as through turgor pressure adjustments and stomatal control. Water potential was intermediate with the combined fertilizer and herbicide treatment. Figure 2 is a plot of 15 herbicide release installations of

FIGURE 1. Pre-dawn water potential at the Johnsrud site.

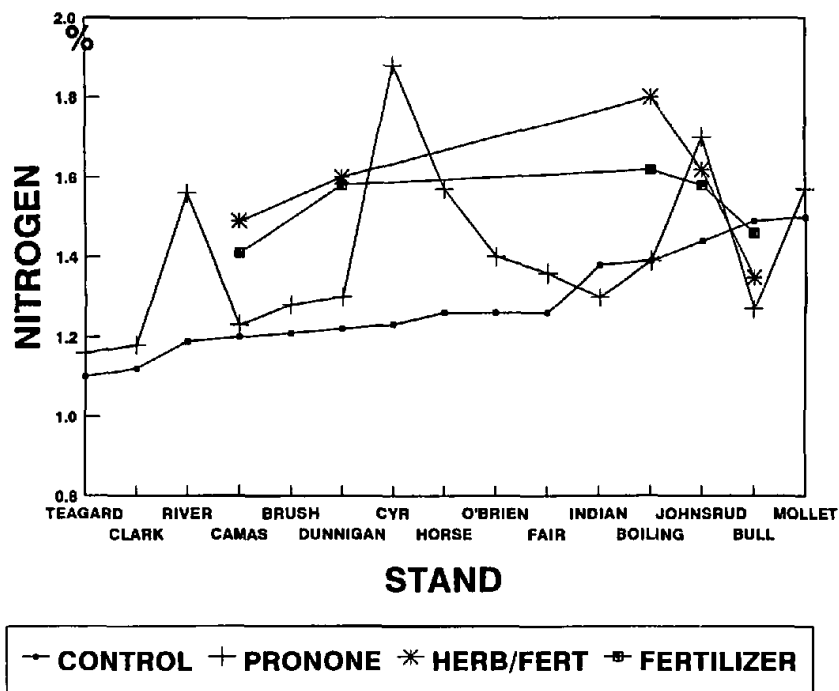


which four had the combined treatments described above. These installations are displayed from left to right on the graph in ascending order of control foliar nitrogen. Note that herbicide control of the understory usually resulted in increased foliar nitrogen concentration, suggesting a significant reduction in competition for nutrients. Substantial tree growth response was measured after two years for all treatments. Similar effects occur with other elements such as potassium. Smethurst et al. (1993) reported similar results for slash pine (*Pinus elliottii* Engelm. var. *elliottii*) in Florida. Understory plants may have a significant role in nutrient cycling; however, other than for N-fixation, nutritional ecology of the understory has been little studied.

Intermountain Forest Tree Nutrition Cooperative Studies

The Intermountain Forest Tree Nutrition Cooperative located at the University of Idaho was organized partially around the presumption that a

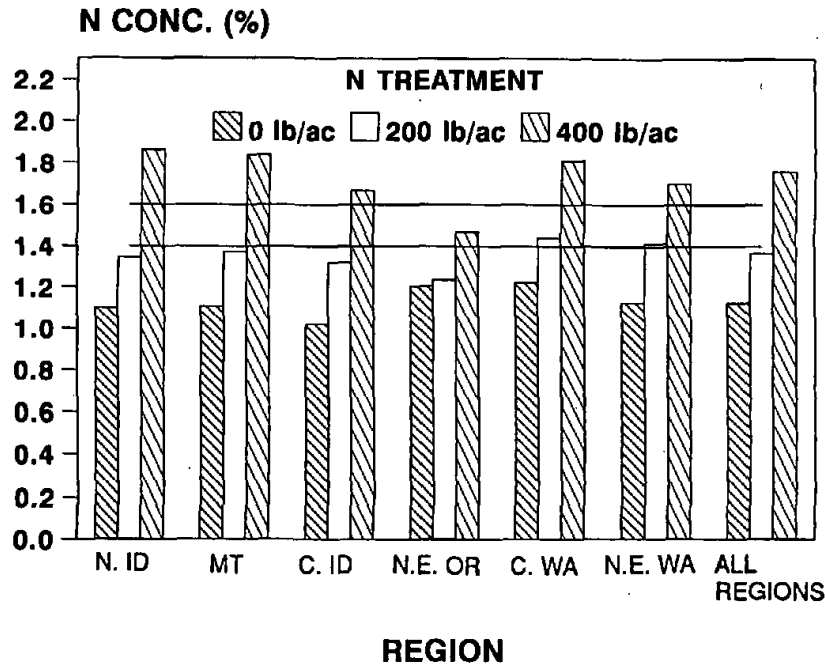
FIGURE 2. Ponderosa pine needle N concentrations for fifteen nutrition study sites in Montana, ranked in ascending order of control plot foliar nitrogen.



simple nitrogen deficiency of inland forests could be documented, thus producing the basis for growth enhancing silvicultural treatment. Figure 3 shows average dormant season foliar N concentrations for various combinations of geographic region and fertilizer treatments within the Inland West. The results show that the presumption of nitrogen deficiency was correct and that nitrogen fertilizer was taken up by the trees, resulting in increased foliar concentrations. Growth rates were also shown to increase significantly for all study regions. While a general dosage-dependent growth response was obtained, some installations produced little or no response, in spite of nitrogen uptake and deficiency.

In an effort to explain why some installations did not respond, pre- and post-treatment tree nutritional status was examined more closely. Evidence pointed to potassium as a nutrient potentially in low supply. Nitrogen application reduced K foliar concentrations and increased N con-

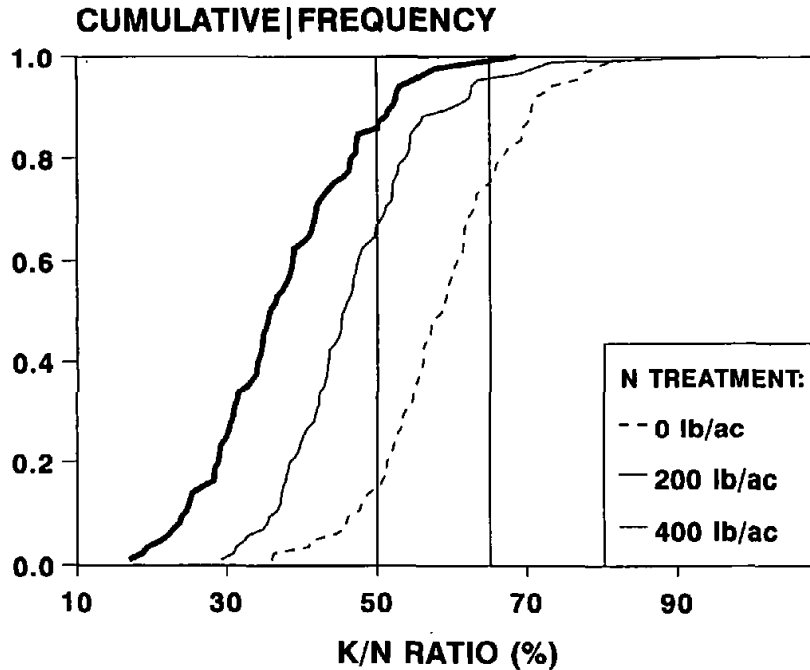
FIGURE 3. Average dormant season foliar N concentrations for the various combinations of geographic region and fertilizer treatment (1.4% N concentrations is inadequate for Douglas-fir).



centrations, thus the K/N ratios were reduced after treatment (Figure 4). Furthermore, post-treatment tree mortality was related to pre-treatment foliar potassium status. While gross growth response was about equal regardless of K nutrition status, net (after mortality) response was greatly reduced on sites with poor pre-treatment K status (Figure 5). This work is reported in detail in Mika and Moore (1991).

In 1987, six fertilizer trials were established in ponderosa pine stands in western Montana. By that time, interest had developed in the potassium-nitrogen relationship such that the IFTNC decided to substitute a nitrogen plus potassium treatment for the higher nitrogen rate treatment that had been standard for the regional ponderosa pine experiment. After four years, two very interesting responses resulted. First, mortality was higher in the plots treated with 200 pounds per acre of nitrogen as urea (200N) than in the 200N + 200K plots. In fact, three of the six installations had

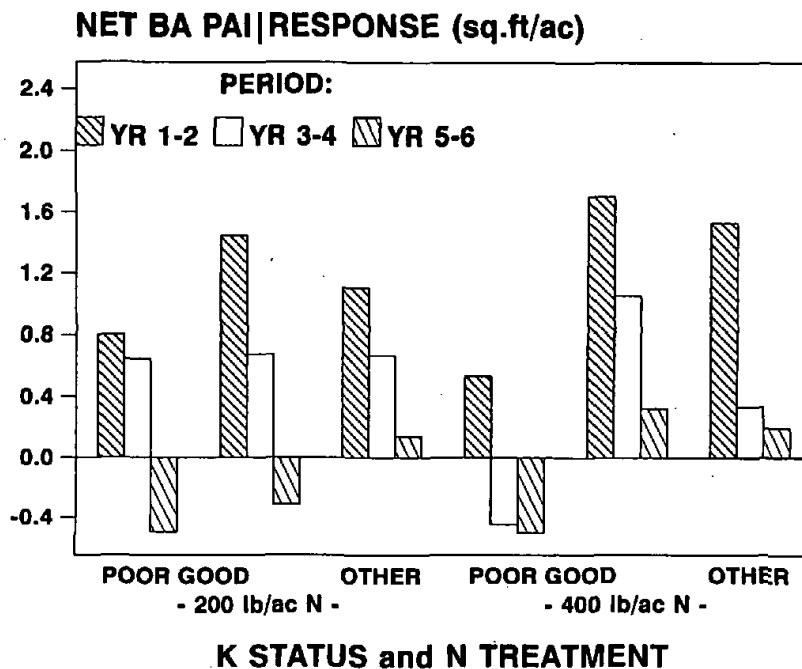
FIGURE 4. The empirical cumulative frequency distribution of the ratio of foliar K and foliar N concentration for Douglas-fir in the Inland Northwest.



negative net growth response to nitrogen alone, but all six installations had positive net growth response to the N + K treatments (Figure 6). Even more interesting was that mountain pine beetles (*Dendroctonus ponderosa* Dougl.) were the primary cause of mortality, and their activities were concentrated in the nitrogen only plots. No trees were lost to beetles in the N + K plots (Figure 7). This work is reported in Mika et al. (1994). Follow-up investigations continue to elucidate what mechanisms "protected" the trees in the N + K plots. A pattern is emerging that indicates potassium deficiency causes inadequate chemical defense compounds to be produced when nitrogen alone is used. There is considerable evidence from agricultural studies documenting a link between plant nutrition, chemistry and incidence of insects or diseases (Huber and Army 1985).

Other results indicate that it may be possible to alter tree root chemistry to the detriment of *Armillaria* root rot by manipulating tree nutritional status. Analysis of mortality patterns in nitrogen fertilized Inland Douglas-

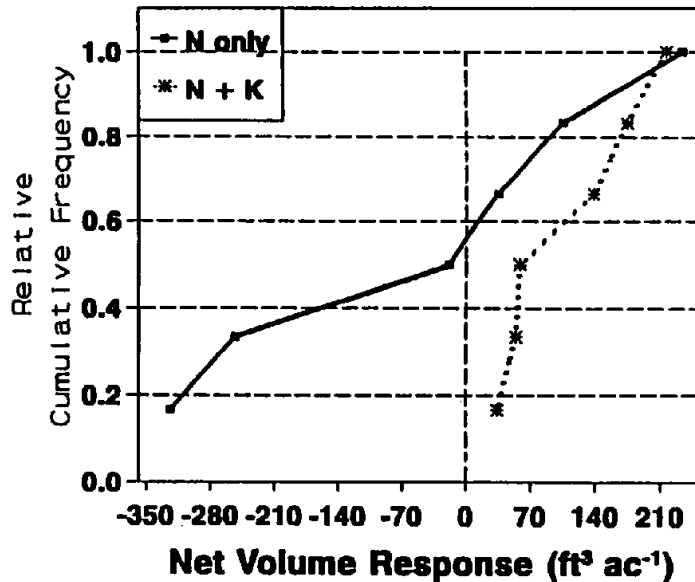
FIGURE 5. Net basal area periodic annual response by 2 yr period for all combinations of fertilizer treatment and K status for Douglas-fir in the Inland Northwest.



fir (*Pseudotsuga menziesii* var. *glauca* [Beissen] Franco) installations showed that much of the mortality was associated with *Armillaria* (*Aemillaria ostoyae* [Romasn.] Herink) root rot (Figure 8). The mortality was greatest in installations with poor foliar K status and in plots with 400 N treatments when compared with those sites having good pre-treatment foliar K status.

Work by Entry et al. (1991) may explain the physiological basis for the root rot mortality and for favorable N + K fertilization results. They investigated some previously installed fertilizer trials in northern Idaho and inoculated trees located in the treatments with *Armillaria* root rot. They found that fertilizer-induced *Armillaria* infection was greatest on thinned and nitrogen fertilized plots and that it was related to root chemistry. Tree roots from thinned-only stands contained high concentrations of phenols and low sugar concentrations while nitrogen fertilized trees had high root sugar concentrations. The ratio of phenols to sugars was strongly corre-

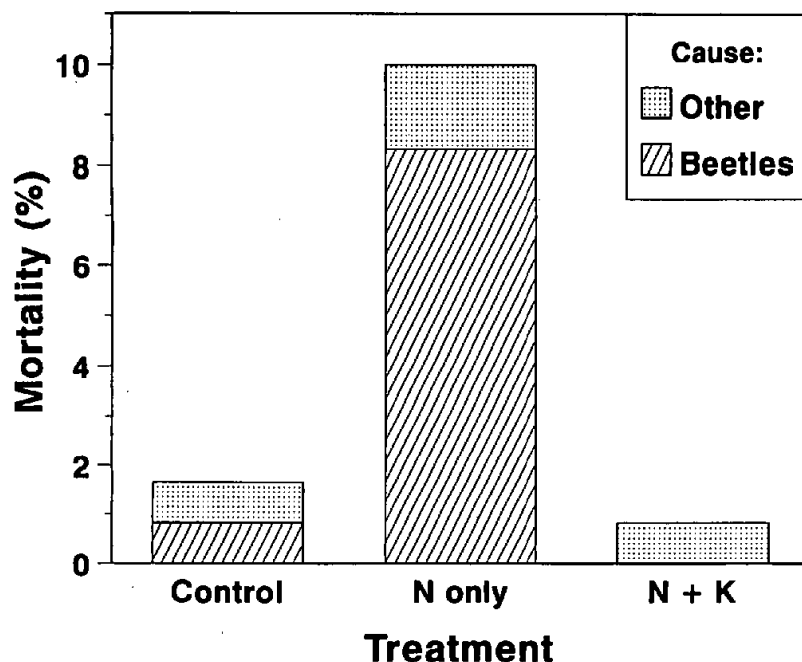
FIGURE 6. The cumulative frequency distribution for net volume response to N or N + K fertilization for ponderosa pine in western Montana. The horizontal axis shows values of response obtained while the vertical axis indicates the proportion of all stands responding at that rate or less. The solid line shows the results for N fertilization while the dotted lines shows N + K fertilization results.



lated to incidence of *Armillaria* infection (Figure 9). Several IFTNC cooperators established nutrition experiments including combinations of nitrogen and potassium fertilizer treatments in Douglas-fir stands with active *Armillaria* infestation. Four years after the fertilizer treatments were applied, root samples were collected and analyzed using methods similar to Entry et al. (1991). The root phenol/sugar ratios by treatment are provided in Figure 10. These ratios are proportional to Entry et al.'s values shown in Figure 9. Potassium treatments significantly increased the root phenol/sugar ratio. Given that a high ratio is bad for the fungus and good for the trees, this experiment demonstrates that it may be possible to change tree root chemistry to the detriment of *Armillaria* by manipulating tree nutritional status (Moore et al. 1993).

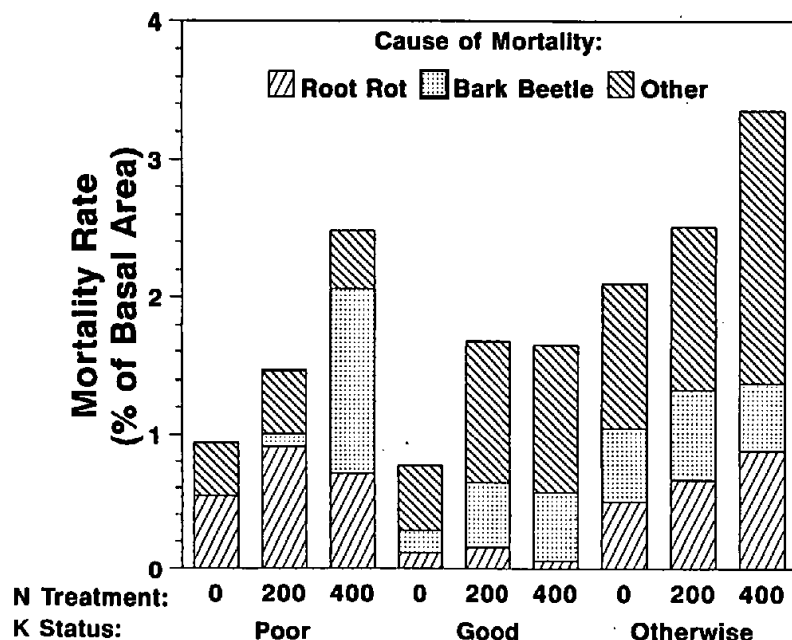
Ylimarto (1991), in a study with Scots pine, found that scleroderris stem canker of seedlings was related to N and K fertilization regimes. Burdon (1991) described the selection pressure applied by fungal patho-

FIGURE 7. Percentage of trees dying in 4 years by fertilizer treatment and cause of mortality for ponderosa pine in western Montana.



gens in plant populations. Waring et al. (1987) suggested that in mountain hemlock stands of the Oregon cascades, increases in nutrient availability and light, following death of the mature forest caused by the root rot fungus *Phellinus weirii* (Murr.) Gilbeatson, increased resistance of young replacement trees to infection by the pathogen. Dmitri (1977) stated that "As in human or veterinary medicine insufficient or excess nutrition of forest plants often leads to disease." Arbitrary fertilizer dressings, often applied without prior soil or needle analysis, may have more negative than positive results. But there is impressive evidence that stand improvement and fertilizer applications according to site, tree species and stand age can contribute to increasing "ecological resistance and health of the system." Garraway (1975) helped elucidate the effects of root chemistry on *Armillaria mellea* (Vahl:Fr.) Kummer thallus growth by demonstrating the superiority of glucose in growth media over other sugars and starch. Singh (1983) reported that nutrient deficient soil media of low pH produced

FIGURE 8. Percent basal area mortality six years after nitrogen fertilization by cause, treatment, and pre-treatment foliar potassium status for a region-wide Douglas-fir experiment.

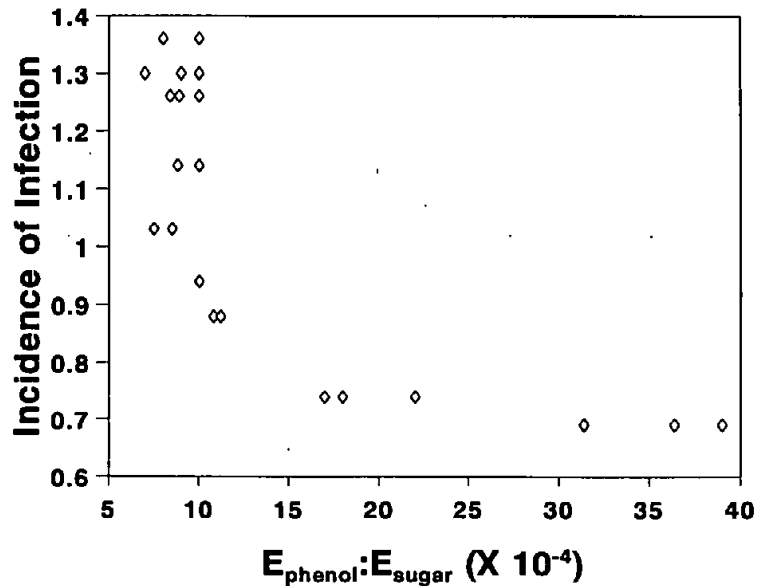


smaller, less vigorous conifer seedlings and the nutrient deficient seedlings incurred greater infection and mortality from *Armillaria*.

Other Investigations

Investigation of the relationships between defoliating insects and tree nutrient status and physiological defense mechanisms has been pursued to some extent. Mason et al. (1992) fertilized Douglas-fir and grand fir (*Abies grandis* [Doug.] Forbes) stands with nitrogen during a period of heavy infestation by spruce budworm (*Christoneura occidentalis* Freeman). They found that both populations and individual spruce budworm larvae increased in size. The trees, though, responded by producing more foliage and increased stem growth, thus indicating compensation by fertilization for defoliation effects. Waring et al. (1992) found that foliage enriched in amino acids due to nitrogen fertilizations increased

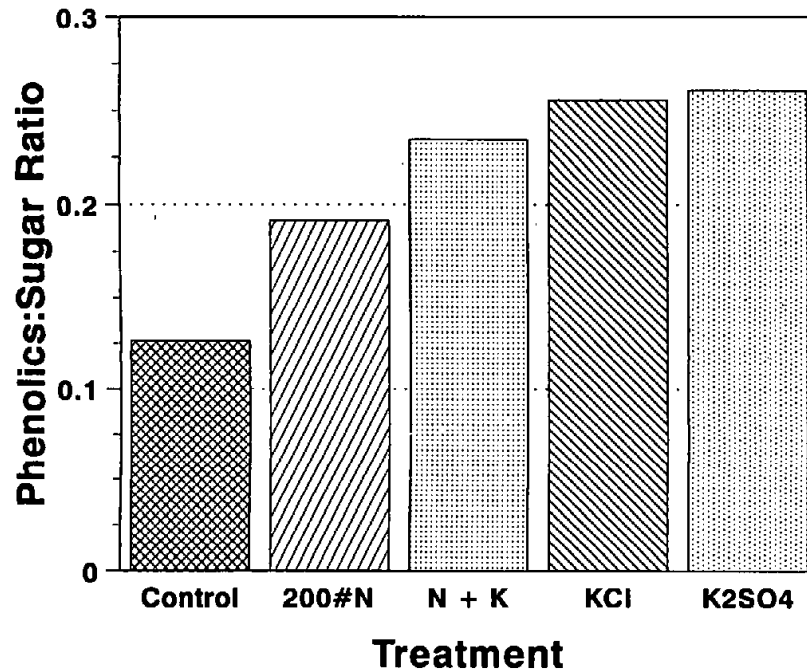
FIGURE 9. Incidence of *Armillaria ostoyae* infection of Douglas-fir versus the ratio of the energy available from root sugar concentrations. From Entry et al. 1991.



Adapted from Entry et al 1991

shoot growth more than enough to compensate for improved nutrition of budworm larvae and consequent increased feeding. Clancy et al. (1988) investigated the effect of seasonal and interspecific variation in foliar nutrients on spruce budworm performance. They suggest that foliar nutrition may be a key factor in budworm feeding behavior. Joseph et al. (1993), working with gypsy moth (*Lymantria dispar* L.) feeding on Douglas-fir in Oregon, found that increased foliar nitrogen improved larval growth and survival. However, high phenolics were shown to be lethal to gypsy moth larvae. Chiu et al. (1992) investigated Douglas-fir needles from treated and untreated IFTNC plots. Nitrogen and potassium treatments usually changed foliage color from green to a blue green (glaucous). It was found that the epicuticular wax changed to a different tubular, ornate morphology (waxes are phenolic compounds). Such structures may have beneficial effects on resistance to sunscald, to water loss and to pests.

FIGURE 10. Douglas-fir root phenolic/sugar concentration ratios four years after fertilization treatments.



RESEARCH NEEDS

The following is a list of research focus areas that we feel will improve our understanding of forest nutrition's role in the health of Inland Western forests.

1. *Followups of Existing Nutrition Trials.* Much has been learned from IFTNC and other fertilizer trials in this and other regions. The original focus of these efforts was timber production, but they are well designed forest nutrition experiments and we can make many inferences for forest health ramifications of nutrition management.
2. *Designs for Future Nutrition /Forest Health Studies.* IFTNC has now developed installation designs that will help us understand the potential of forest nutrition management to deal with *Armillaria* root disease, bark beetles and other mortality causing agents. Optimum

nutrition trials (response surfaces) are a planned first step. This effort should be expanded.

3. *Inland Western Nutrient Cycling Studies*. Basic nutrient cycling studies are needed across a variety of sites, especially those experiencing health problems.
4. *Genetics in Forest Nutrition*. One issue in forest health is the loss of seral species from our forest communities. We need more information regarding how these species shifts affect nutrient cycling and the implications of those changes for forest health. Also, perhaps most importantly, it is recognized that there is substantial genetic control of nutrient uptake at both the species and intraspecific levels. More work is needed in this area of genetic/nutrition/forest health ecology.
5. *Collaborative Studies Between Forest Pathologists, Entomologists, Geneticists, and Physiologists with Forest Nutrition and Soil Scientists*. We feel that we have given some good examples of successful cross discipline efforts and strongly suggest that more be undertaken.

CONCLUSIONS

We must decide how, in managing forest ecosystems and their health in this Region, we can utilize what we have learned about forest nutrition. We have several suggestions for immediate application to forest management operations including forest harvesting, thinning, fertilization and prescribed fire. Nutrients should be conserved, particularly on nutrient poor sites, by learning tree foliage and branches on the site; fire should be reintroduced where possible and appropriate; and sometimes site nutrient capital will need to be restored through forest fertilization. We feel that a fundamental understanding of forest nutrition will be integral to developing effective solutions to the Inland Western forest health problems.

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